INSECTS AND THE SPECTRUM

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In the JOURNAL OF THE NEW YORK ENTOMOLOGICAL SOCIETY for September, 1944 (vol. 52, p. 267–271), under the title "Insect Responses to Colors," the results of various workers were summarized, showing that both the electrical responses of the insect eye and the motor responses of the insect itself to different colors of equal physical intensity are due to differences in sensitivity, or to the absorption of light, which varies with wave-length, by the primary photosensitive substance of the visual sense cells, and are not the effects of wave-length by itself. The investigators, by properly adjusting the intensities, were able to match the response to one color with the response to any other color. Under the stimulus of colors of equal physical intensities the visibility curve for the insect eye is qualitatively similar to the group motor behavior curve of insect response to various wave-lengths in the visible part of the spectrum.

The present article has been written for the purpose of gathering from the literature any additional evidence that may have a bearing on the subject of insect responses to color stimuli. Folsom[1] found that *Aphis gossypii* Glov. occurred in much greater numbers on cotton plants treated with calcium arsenate than on untreated plants. And more evidence of a similar sort in connection with the use of certain insecticides has been accumulated by Gaines *et al.*,[2] Bilby,[3] and by Smith and Fontenot.[4] Both McGarr[5] and Gaines[6] found that although the use of cryolite-sulfur dusts increased the aphid population somewhat, on cotton,

[1] Calcium arsenate as a cause of aphis infestations. Jour. Econ. Ent., 20(6): 840–843, 1927.

[2] Effect of different calcium arsenates upon boll weevils, cotton aphids and plant bugs and upon yields. Jour. Econ. Ent., 34(4): 495–497, 1941.

[3] Cotton investigations in Peru. Jour. Econ. Ent., 35(2): 193–197, 1942.

[4] Notes on the effect of arsenicals upon the cotton aphid, predators and other insects. Jour. Econ. Ent., 35(4): 596, 1942.

[5] Control of the cotton aphid and boll weevil in 1940. Jour. Econ. Ent., 34(4): 580–582, 1941.

[6] See footnote 2.

this increase was much less than when calcium arsenate was used. Hill and Tate[7] found that the aphid *Myzus persicæ* (Sulz.) increased significantly in numbers in experimental and commercial plantings of potatoes where zinc arsenite had been used for controlling the potato flea beetle. Moore[8] in studying the reactions of the potato aphis *Macrosiphum solanifolia* Ash., to unsprayed potato leaves and to potato leaves sprayed with Bordeaux mixture, found that aphids were definitely attracted in larger numbers to sprayed leaves. He also found that there was no difference in the wave-lengths of light reflected from the two leaf surfaces (sprayed and unsprayed), but that the light reflected from the sprayed leaf surface was more intense, and that more of the longer wave-lengths was absorbed by the sprayed leaf.

Moore[9] also reported that *Myzus persicæ* (Sulz.) was attracted to potato plants that had been sprayed with Bordeaux mixture because of the increased intensity of the light reflected from the sprayed surfaces, the numbers of insects appearing to follow the inverse square law of light intensities. He also stated that the cabbage aphid *Brevicoryne brassicæ* L., could be reduced in numbers, below those on untreated plots, by the use of colored dusts. Black dust was the most effective one in reducing the infestations. Moore believes that light intensity is the most important factor in attracting the insects to the sprayed surfaces.

Herms[10] working wih the Clear Lake gnat *Chaoborus lacustris* Freeborn, and electrocuting light traps in which red, green, light-blue, dark-blue, blue, violet, ultra-violet and white lights were used, each of approximately the same intensity, found that almost the same number of gnats was collected from each trap over a given period of time, indicating that the gnats have no selective color response. Herms concluded that the response was due to the intensity and not to differences in wave-lengths of the lights. He found that up to the point of deterrence, the number of insects

[7] Increase in aphid populations on potato plants sprayed with zinc arsenite in western Nebraska. Jour. Econ. Ent., Feb. 1943.

[8] Studies on the reaction of potato aphids to sprayed and unsprayed potato leaves. Jour. Econ. Ent., 28(2): 436–442, 1935.

[9] Reactions of aphids to colored insecticides. Jour. Econ. Ent., 30(2): 306–309, 1937.

[10] The Clear Lake gnat. Univ. of Calif. Bull. 607: 20, 1937.

attracted to a light is directly proportional to the increase in the intensity of that light. In this experiment the wave-lengths ranged from 3500 Å to 7000 Å and the intensities were equalized by using 60-watt lamps for all colors. The wattage of a lamp is not an accurate measurement of the intensity of the energy emitted and the wave-length bands were too broad for anything approaching monochromatic colors. Because of this it is difficult to interpret the results more specifically. Experimental work by others has demonstrated that if the physical intensities of the wave-lengths are really equalized, there is a difference in response to the different colors, although this is due to the absorption of light, which varies with wave-length, by the primary photosensitive substance of the visual sense cells.

Others have found intensity [brilliance] to be important also. Ficht and Hienton,[11] working with European corn borer moths and electric traps, state that certain color bands of the visible spectrum were preferred by the moths, the violet-blue band being the most attractive. These authors found that intensity was an important factor in the attractiveness of the lamp to the moths, the number of moths attracted being in almost direct proportion to the intensity of the light in the visible spectrum. These authors worked with broad bands, *i.e.*, 3800–5000 Å (violet and blue); 5000–6000 Å (green and yellow); 6000–7000 Å (orange and red).

There seems to be little doubt about the ability of many insects to distinguish differences in brightness. According to Bertholf[12] the honeybee "begins to distinguish between two illuminated areas when the intensity of one is reduced to at least 70 per cent of the intensity of the other." He found that in bees "the exact percentage of white light required to equalize a given chromed beam in stimulative effect was very difficult to ascertain accurately," due probably to the inability of the bees to recognize differences in brightness unless they are of some magnitude.

Bertholf first used such low percentages of white that they definitely induced fewer reactions than the chromed beam. Then he

[11] Some of the important factors governing the flight of European corn borer moths to electric traps. Jour. Econ. Ent., 34(5): 599–604, 1941.

[12] Reactions of the honeybee to light. Jour. Agric. Res., 42(7): 379–419, 1931.

gradually increased the intensity of the white by small steps "until it definitely induced more reactions than the chromed beam." He then was able to select a point which fairly represented "the percentage of white that just equalled the chroma in stimulative effect."

From an extensive and carefully conducted traplight experiment involving 660 species represented by 12,869 specimens and from the utilization of only such of the species that entered the traps in statistically significant numbers Milne and Milne (1944) draw certain conclusions among which are the following: "Difference in response to any given set of colored lights is on a specific basis, not a generic or family basis. Thus some insects definitely see red light, even if the honeybee does not." "Some species respond primarily to brilliance. This is not true of the preponderance of species. Traps of the same color but different brilliance are not selected chiefly on the basis of intensity." "Preference for one color over another by a species seems to be somewhat independent of brilliancy (at least within the range of brilliancy investigated in these experiments), but the relative attraction of unbalanced white and a color depends to some extent on the difference in light output between the two. Because all lights were alike except for colored coatings on some which removed some wave-lengths, the experiments where the insects selected a dull light in preference to a bright one, are clearly independent of the spectral luminosity function of the insect eye."

These authors admit that more control of wave-length would have been desirable and that their attracting lights should have been more monochromatic, but the use of small filters was not feasible in view of the high intensity needed for outdoor experiments. From the behavior of the species that came under their observation and from their careful analysis of the results I do not see how their conclusions could have been other than what they are.

In view of my own work, however, I cannot agree with them that the response to colored lights is on a specific basis. I found that the group behavior pattern to colored lights of equal physical intensity was essentially the same for many species in several orders; also that there was a shifting of individuals from one light to another during each test, but that the behavior of the group was fairly constant during each test. In other words, some individuals that went to ultra-violet on the first test would go to green on the second and perhaps blue on the third, but at the end of each test the proportion of the total that went to each color was practically the same. Since individual insects are erratic photometers, this may explain why the Milnes' traplight species behaved the way they did.

The Milnes also conclude that although some species respond primarily to brilliance, this it not true for the preponderance of species. My own opinion, based upon the fact that I could change the group behavior response by increasing the brilliance of the colors and upon the work of Crescitelli and Jahn (1939) on the electrical responses of insect eyes to different qualities of light, leads me to believe that of the two, brilliance or intensity is probably more important than wave-length in initiating responses to various wave-lengths in the spectrum to which insects react. Insects will react positively to all wave-lengths from approximately 3650 Å to 7200 Å, the shorter wave-lengths usually requiring much less intensity than the longer ones in bringing about a positive response. This is due to the greater sensitivity of the insects to the shorter wave-lengths. An insect's reaction to light, colored or white depends upon its sensitivity at a particular time, upon the intensity of the wave-lengths to which it is first exposed, the angle of incidence, temperature, moisture, air currents, etc., and in its natural state it is not as good a photometer as a group of laboratory specimens over which one has some control.

Donald L. Collins (Jour. Exp. Zool., 69(2): 165–185, 1934), insofar as the codling moth is concerned, found that the nature of the moth's reactions to constant, or changing light varied according to the position of the iris pigment and he believes that the iris pigment migrations are important in determining the behavior. It is known that the movement of the iris pigment in the eyes of nocturnal insects does not occur instantly or at all speedily. Under natural conditions the movement is gradual. If, when the pigment is in a position to admit as much dim light as possible, the nocturnal insect is exposed to a bright light, the pigment does not respond rapidly enough to exclude the brightness and as a result the insect is stimulated far beyond its normal night behavior. This continues until the pigment moves to a position wherein the brightness is intercepted. This iris pigment movement appears to have a bearing upon light-trap captures.

On the basis of the results reported upon in the paper entitled "Insect Responses to Colors" together with some of those just summarized, it is apparent that insects when exposed to a spectrum of equalized physical intensities extending from 3650 Å to 7200 Å, behave as if they have color preferences. The stimulating efficiency increases slightly from zero at 7200Å to 5700 Å from where it rises to a maximum of 4920 Å in the visible spectrum. It then declines to a low level at 4640 Å from which point it ascends to a peak maximum at 3650 Å. However, such reactions to colors of equalized intensities instead of being interpreted as color preferences may be looked upon as representing the absorption spectrum of the primary photosensitive substance of the visual sense cells. The absorption of light by this substance varies with wave-length and the production of a given response needs a certain amount of photochemical change which in turn requires the absorption of a constant amount of energy. Thus it is seen that a wave-length stimulus possesses both a physical and a physiological intensity and that although the physical intensities of wave-lengths may be equalized, the physiological intensities produce different effects due to the fact that the absorption of light by the primary photosensitive substance in the visual sense cells, varies with wave-length.

The same results that were obtained by exposing the insects to a spectrum of equalized physical intensities from 3650 Å to 7200 Å, could by inference from the work of Bertholf and others, be obtained by exposing them to a series of white lights properly adjusted in physical intensities.

The ability to distinguish one color from another is not proof of color vision unless the colors are of equal brilliance to the insect. Just what constitutes brilliance to an insect is unknown. Ultra-violet, which is very effective in producing a positive reaction, is black to us. In the work of Weiss *et al.*, the physical intensities of the wave-lengths were equalized but the brilliance of each varied and it was the combination of wave-length and intensity that either initiated or failed to initiate a response.

When insects are confronted by wave-length bands, of equalized physical intensities, from 3650 Å to 7200 Å, the primary photosensitive substance of their visual sense cells absorbs the energy at 3650 Å to a greater extent than the energy at other wave-lengths. Ultra-violet light as well as other short wave-lengths of light contain more energy than the longer wave-lengths and chemical reactions are produced more readily by them. The resulting photochemical reaction is accompanied by physical changes in nerve fibers including a change in the electrical activity which is finally transmitted to the muscles. [The theory of the electrical transmission of nerve impulses to effector organs has been superseded by the factual demonstration of chemical transmission. See ''Chemical Transmission of Nerve Impulses'' by Otto Loewi, American Scientist, 33(3): 159–174, 1945.] As a result insects are particularly sensitive to ultra-violet light of 3650 Å and react positively in greater numbers to this wave-length in preference to all others of equal physical intensity provided it is not intense enough to cause repellency. It is also true that the photosensitive substance of the visual sense cells of insects will function at any wave-length between 3650 Å and 7200 Å if the physical intensity of the wave-length is sufficient and constant.

On the basis of the importance of intensity [brilliance] as set forth by the authors of various laboratory and field tests, one wonders if color has any significance to insects if the intensity or luminosity of any wave-length is sufficient to elicit a response. On the other hand, many flower-visiting insects behave as if they have color perception. There is the work of Lubbock, Forel, Frisch, Lutz, etc., in training bees to associate the finding of food with certain colors, and the work of Bertholf upon the stimulating effect of different wave-lengths in the ultra-violet and visible spectra and upon training bees to distinguish differences in chromas of the same brightness associated with food. Numerous other observations involving butterflies and colored paper flowers and colored papers and the behavior of other insects tested by the use of the optomotor reaction are summarized by

Wigglesworth (1934) to indicate that color vision exists in many other insects. In some of these tests, however, nothing is reported to show that the workers knew what spectral colors were actually reflected from their colored flowers and papers and the results as a whole show a diversity of behavior which it is hard to believe exists. It is also difficult for some observers to divorce themselves from their own color sensations and to realize that insect sensitivity to a spectrum extending from about 3650 Å to 7200 Å makes it unwise to explain their reactions in terms of human color vision.

Lutz found that few flowers reflect any considerable proportion of ultra-violet. Of the 25 flowers studied only 4 were found to reflect more than 10 per cent of radiation shorter than 3800Å. Quoting from his paper—"All colors of the spectrum from red to ultra-violet inclusive are found in light reflected by one flower or another. Of these light waves reflected by flowers, those of relatively great length, red to green are more common than those of shorter length, blue to violet. Flower-visiting insects do not 'see' red to green as well as they do blue to ultraviolet." Since this was written it has been demonstrated that they do "see" the longer wave-lengths if the intensities are strong enough. Lutz's work with ultra-violet and flower-visiting insects did not, as he has stated, show that ultra-violet flowers are more attractive to insects, but that ultra-violet is a "color" to insects just as red is a color to man. He found that ultra-violet flowers were no more popular with insects than flowers reflecting colors visible to humans.

It is not thought that insects depend as much upon their sense of sight as they do upon their sense of smell and one wonders if their activities that appear to be associated with colors could not be initiated by luminosity or brightness alone in combination with any wave-length of the spectrum to which they are sensitive, so long as it was intense or bright enough to be absorbed. The question then arises as to why, when a group of insects is exposed to various wave-lengths of equal physical intensities from 3650 Å to 7200 Å, all do not go to ultra-violet which is presumably the brightest. This can only be answered by saying that not all individual insects are in the same physiological state at the same time and that there exist some variations by individuals in the sensitivity of their visual receptors. Such variations may be due to a depletion of the primary photosensitive substance in the visual sense cells resulting in a positive movement to lower illuminations. Until restorative processes take place in the visual sense cells of such individuals, their sensitivity to ultra-violet declines. In the experimental work of Weiss *et al.,* it was observed that there was a shifting of individuals that went to the different wave-lengths, in successive tests, but little difference between the final group behavior results of each test.

The assumption that insects might react positively only to different degrees of brightness regardless of wave-length would mean that the investigators who trained bees to come to different colors for food and to color patterns marking the site of their nests—were really training these insects to associate different reflected degrees of luminosity or luminosity patterns with their food or nest. In the same way it would have to be assumed that flower-visiting insects, and others, insofar as they depend upon vision to find sources of nectar and food, locate these by means of reflected luminosity, the juxtaposition of the little reflected luminous areas of variable intensity and quality received by the ommatidia giving rise to some sort of contrast between the flower and its surroundings.

Butterflies require several days' training before they will associate particular colors with the presence of food and after an interval of one day only traces of the acquired response remain.[13] Bees may be trained in as little as two hours and they may retain this training for four days.[14] Among the Hymenoptera visual and olfactory memory are important in enabling the insects to find their way to and from their nests.

Learning in insects is usually connected with the association of an unaccustomed stimulus with a common stimulus to which there is an established reaction, the newly acquired habit being called a conditioned reflex. "If an insect appears to 'learn' or to give a certain reaction after a number of repetitions, it is supposed that some primary resistance in the synapse has been

[13] Ilse, D. Z. vergl. Physiol., 8: 658–692, 1928.

[14] v. Frisch, K. Zool. Jahrb. Physiol., 35: 1–182, 1914.

broken down and that the conduction of the stimulus over the same tract in the central nervous system becomes smoother and finally automatic.''[15]

Brues, who studied the color patterns of butterflies by photography in ultra-violet light, concludes, ''That the visual picture of butterflies produced in the human eye differs in varying degrees from photographs made by reflected ultra-violet light. A range of 3300 Å to 5900 Å which includes some ultra-violet that is photographically very active (3650 Å) appears to approach the human image very closely, and theoretically at least should represent the image in the insect eye. It follows that certain red and orange markings are readily visible to insects on account of the ultra-violet that they reflect and not by reason of the reflected orange or red which affects our own eyes.'' Whether the image is seen by the insects in colors or as reflected luminous areas of variable brightness is not known but if the red and orange markings reflected ultra-violet, this wave-length might appear brightest to the insect. In any event insects are particularly sensitive to this color. On the other hand, there is no reason why orange or red that did not reflect ultra-violet could not elicit a response from an insect if the reflected intensities of these colors were strong enough.

In conclusion, it appears that of the two inseparable constituents, wave-length and intensity, the latter seems to be the most important in producing reactions. As color and brightness are forms of consciousness and as it is impossible to definitely interpret insect behavior into any such kind of awareness, I am inclined to agree with Snodgrass that this particular phase of the subject is hardly worth discussing because the facts cannot be known.

The following bibliography is supplementary to the one published in the Journal of Economic Entomology, 36(1) : 1–17, 1943.

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[15] Snodgrass, R. E. Principles of Insect Morphology, New York, 1935.

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